

Discrimination and phenology of hilltopping butterflies on two mountains on the boundary between Osaka and Nara Prefectures, central Japan

Sophie NAVEZ* and Minoru ISHII

Entomological Laboratory, Graduate School of Agriculture and Biological Sciences,
Osaka Prefecture University, Gakuen-cho 1-1, Sakai, Osaka, 599-8531 Japan

Abstract In order to discriminate hilltopping butterflies and elucidate their phenology, we fixed, respectively, 46 and 26 5-m radius virtual circles on the summit, subsummit and slope of Mt Katsuragi (960 m alt.) and Mt Nijo (2 peaks: Medake, 474 m alt. and Otake, 517 m alt.) located on the boundary between Osaka and Nara Prefectures, central Japan. During annual surveys from spring to autumn in 2001–2002 on Mt Katsuragi and in 2002 on Mt Nijo, we used the mean frequency of visits during 5 min census periods in each observation circle as quantification method. A total of 55 species (8 families) were observed and 29 species were common to the 3 peaks, with 53 species seen in Mt Katsuragi, 42 in Medake and 31 in Otake. On both mountains, most species were rare (low abundance). According to 2001 results from Mt Katsuragi, *Papilio machaon*, *Argyreus hyperbius*, *Libythea celtis*, *Colias erate* and *Lycaena phlaeas* were classified as hilltoppers because their distributions were statistically biased on the “broad summit” (including summit and subsummit circles). However, the hilltopper status of the last three species remains controversial. On Mt Nijo 2002, *Vanessa indica*, *Cynthia cardui*, *P. machaon*, *Papilio xuthus*, *Papilio bianor*, *Papilio helenus*, *Nymphalis xanthomelas*, *A. hyperbius*, *Lampides boeticus* and *Hestina japonica* were hilltopping. Although all those species were also recorded on Mt Katsuragi, data from 2001 and 2002 confirm that, on Mt Katsuragi, *P. xuthus*, *P. bianor*, *P. helenus* and *H. japonica* were not hilltopping. All other Nijo’s hilltoppers were also hilltopping in Mt Katsuragi (2001 and/or 2002 data). On the contrary, *Parnara guttata* and *Luehdorfia japonica* were hilltopping on Mt Katsuragi in 2002 but not on Mt Nijo, where *L. japonica* was not recorded. *C. erate*, *L. phlaeas* and *L. celtis* were not hilltoppers on Mt Nijo. *P. xuthus*, *H. japonica* and *C. cardui* were hilltopping on Medake but not on Otake. Though some hilltopping species were very abundant on the summit in the 3 seasons (*P. machaon*), or only 2 seasons (summer and autumn for *A. hyperbius*, spring and summer for *C. erate* and *L. celtis*) or 1 season (autumn for *L. boeticus* and *P. guttata*), variation existed between peaks concerning the dominance ranking order of those species. On the other hand, some hilltoppers such as *V. indica*, were rare or relatively rare on the 3 peaks in the 3 seasons, though still presenting some variability in relative abundance and dominance ranking status between peaks.

Key words Butterfly, Hilltopping, Mt Katsuragi, Mt Nijo, seasonal abundance, Japan.

Introduction

Hilltopping in butterflies is traditionally viewed as a behaviour in which males and virgin females seek and congregate on a prominence from the surrounding environment to mate (Shields, 1967; Lederhouse, 1982; Wickman, 1988). Low density species and species whose receptive females are widely dispersed in space and time practice the behaviour in order to produce enough individuals at each generation to mate (Shields, 1967; Scott, 1968; Alcock, 1983; Rutowski and Alcock, 1989). Hilltopping would be a default strategy, called male dominance polygyny, used by males when neither females nor the resources they use are clumped and thus cannot be economically monopolized by males at potential feeding, oviposition or emergence sites (Rutowski and Alcock, 1989). The female orientation hy-

*Corresponding author. E-mail: snavez@hotmail.com

pothesis was suggested for explaining why peaktops would become rendezvous points (Alcock, 1987). Males were shown to adopt either a (non) territorial perching, patrolling or both mate-locating tactics (*e. g. Papilio zelicaon*) on hilltops (Shields, 1967).

However, previous studies involving hilltopping butterflies focused on only one hilltop at a time and on the behavioural and distributional comparison of species from different taxonomic groups (*e. g.* butterflies with bees, wasps, and flies) present on that hilltop (*e. g.* Alcock, 1983, 1984, 1985) or on only a small number of butterfly species pertaining to the same genus (*e. g. Vanessa* spp. in Brown and Alcock, 1990) or family (*e. g.* Papilionidae in Pinheiro (1990(91)) and Turner (1990)). Thus it is necessary to make comparison among exclusively butterfly species (same and different families), among peaks, among seasons and among zones (summit, subsummit and slope) in each mountain to clarify if hilltopping is a unique/standardized phenomenon with only one purpose and generated by only one set of factors.

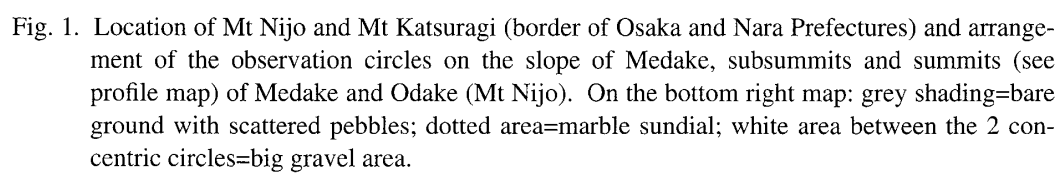
The present study was done to make the total list of species recorded on two mountains (and 3 hilltops) in Central Japan, and to identify which ones might be considered as (non) hilltoppers. Besides, it will check whether some species hilltop on one mountain but not on another in spite of the species' presence on both mountains. Butterflies are selected among other possible hilltopping groups such as Diptera, Hymenoptera, Coleoptera or Orthoptera (Shields, 1967) because of their easy survey, well-known taxonomy, ecology, ethology and life-cycle as well as their reputation as good indicator taxa whose incidence and abundance reflect even slight modifications in their environment (New, 1993). Sites belonging to the same geographical area (*i. e.* in the same type of landscape) will be chosen for comparison. Otherwise, other landmark, non-resource encounter sites than hilltops (*e. g.* forest-meadow edges, vegetation funnels, sidewalks, forest clearings, gullies) might be used by species if the geographically separated area displays (nearly) no hills in its landscape (Rutowski and Alcock, 1989; Brown and Alcock, 1990 (91); Alcock and Gwynne, 1988; Bitzer and Shaw, 1979). The three hilltops will also be selected according to their altitudinal differences, distinct topography (small, flat hilltops *vs* large, undulating ones) and contrasting vegetation types (forest edge *vs* bare-grassy).

Study sites and methods

a) Study sites and schedule

The study was first conducted for 34 days from April 23 to October 25, 2001 on Mt Katsuragi (or Yamato-Katsuragi) (960 m alt) located at the frontier between Osaka and Nara Prefectures, central Japan (Fig. 1). The site vegetation was mainly characterized by deciduous broadleaved forests and coniferous plantations of Japanese cedar (*Cryptomeria japonica*) and cypress (*Chamaecyparis obtusa*) on the slopes, by bare and grassy (dominated by bamboo grass *Pleioblastus chino* and *Miscanthus sinensis*) ground on the hilltop and by thickets of shrubs (especially *Rhododendron* spp. on the upper half of southern slope) mixed with bamboo grass on the beginning of slopes surrounding the hilltop.

We fixed 46 observation points at different altitudinal levels on the hill and on different transects, and the frequency of visits (see definition below) for any encountered butterfly species within the range of 5-m radius circles around the 46 points (observation circles) (Fig. 2) was recorded (1 census session/day) during 10 min census periods in each circle from, on average, 9h30 to 15h30. The forest transect circles (slope) were observed on another day, in alternance with the summit and beginning of slopes (subsummit) censuses sessions. Each day a different itinerary for the 46 circles was followed so as to minimize the



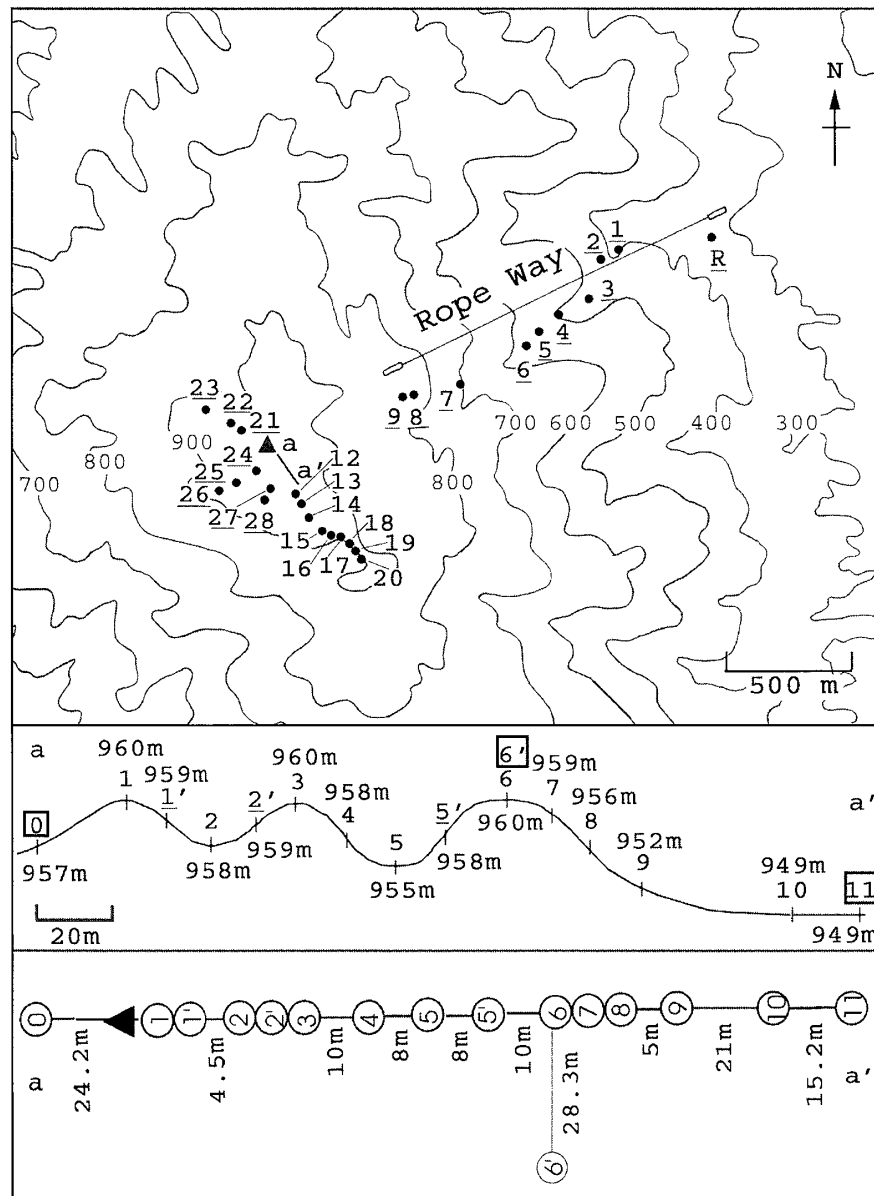


Fig. 2. Arrangement of the observation circles along the slope, subsummits and summit of Mt Katsuragi. A microtopographical profile of the summit transect is also shown. Numbers framed by a square are circles checked only in 2002. The underscored numbers represent circles checked only in 2001. On the lower map, circled numbers depict 5-m radius observation circles.

bias associated with the time of day when records are taken at a particular location on the hill. In 2001, 40 circles out of 46 were observed.

In 2002, a similar study was carried out in alternance (every two weeks) on two mountains belonging to the same Kongo-Ikoma mountain range, Mt Katsuragi and Mt Nijo (extinct volcano with 2 peaks separated by a saddle (431 m alt): Odake (517 m alt) and Medake (474 m alt)), for 75 days spanning three seasons from April 8 to October 16 (Figs 1, 2). On Mt Katsuragi, 22 circles out of 46 were checked while, on Mt Nijo, 26 circles were fixed and checked. Mt Nijo was also covered by deciduous broadleaved forest and conifer plantations on the slopes, but the slope transect was much more open and sunny than on Mt

Katsuragi, due to the presence of huge volcanic rocks spreading on certain slope sections. The two peaks of Mt Nijo had lightly forested hilltops composed mainly of cherry trees and oaks with some ornamental shrubs.

In Nijo and Katsuragi 2002, the observations started earlier (from 8h30 or 9h00) and ended later (18h00) and 5 sessions/day (every two hours) with 5 min/census instead of 10 min were used. Besides, in Katsuragi 2002, summit and subsummit transects were censused on different days and, in Nijo 2002, one day was spent only on Medake summit plus subsummit (10 circles), another day only on Odake summit plus subsummit (10 circles) and still another day for only the slope transect (6 circles). For the slope transect in Nijo 2002, 3 sessions/day instead of 5 were used, with early beginning or later beginning census days, in alternance, in order to compensate for missing periods and get the full range schedule. However, since the weather was not so stable every day, some sessions in both mountains are sometimes missing and the number of days spent on each (sub)summit or slope transects also varies according to available weather conditions during the year.

b) Quantification method

The frequency of visits in each circle by individuals (males and rare females) involved in any activity related to mating behaviour was used as an index of preference for that circle. Alcock (1984) also used that index in the case of non territorial percher and patroller species on a hilltop. One “visit” record consisted of a specimen entering a circle, or entering and directly leaving a circle, or only of a specimen being already present at rest in the circle. The behavioural categories included within observed “mating behaviour” were: perching, patrolling, intermediate between perching and patrolling, fights (or just investigative chases), courtship, mating pairs. Foraging and indeterminate behaviours were excluded from the counts. Perching and patrolling individuals were distinguished from simply resting, basking or passing individuals using the criteria cited in: Alcock, 1984; Alcock and Gwynne, 1988; Alcock and O'Neill, 1986; Bitzer and Shaw, 1979; Brown and Alcock, 1990 (91); Dennis and Williams, 1987; Kemp, 2001; Lederhouse, 1982; Pinheiro, 1990(91); Scott, 1974, 1975; Shields, 1967; Williams, 1994.

Altitude was measured in the centre of each circle with a GPS device (Garmin, eTrex Summit) having been first calibrated on the known altitude of the highest point of each summit. Only fragmentary, qualitative data on the presence and distribution of certain larval foodplants and nectar sources were collected (Table 1). Statistical analysis was performed with SPSS 12.0 for Windows software package. Daily air temperatures (at 10 min intervals) were measured by one Optic StowAway data-logger (BoxCar 3.7 for Windows) placed in the shade at 1.5 m above the ground on Mt Katsuragi and Medake summits, respectively.

Among the list of butterfly species in Table 2 (see Results), only those which 1) had enough counts to be analysed statistically and 2) were known or potential candidates for hilltopping in the literature or were unambiguously abundantly concentrated on summit areas of one or both mountains, were selected. Determination of the (non) hilltopping status of species was realized with data from Mt Katsuragi in 2001 and/or Mt Nijo in 2002 (Table 4). Chi-Square goodness-of-fit tests were used to determine whether each species considered is randomly distributed on the hill or not. When $N/k < 5$ (N =total number of visits for each species; k =number of observation circles), the test cannot be trusted to make appropriate inferences (Siegel and Castellan, 1988). In order to render the test valid again, expected frequencies were increased by combining pairs of circles into single pooled circles, in a meaningful way (*i. e.* equivalent circles together, such as circles at more or less the same altitude).

Table 1. List of foodplants (fp) and commonly used nectar sources (ns) for hilltopper butterflies on Mt Katsuragi, and Medake and Odake Peaks of Mt Nijo; ++ abundant, + rare, – none

Plant name	Katsuragi	Medake	Odake	Notes
Umbelliferae				
<i>Angelica pubescens</i>	+	–	–	fp for <i>P. machaon</i> (2 events of oviposition + presence of eggs and larvae)
<i>Angelica decursiva</i>	+	–	–	fp for <i>P. machaon</i>
<i>Ostericum sieboldii</i>	+	–	–	fp for <i>P. machaon</i>
Compositae				
<i>Artemisia princeps</i>	++	+	+	fp for <i>C. cardui</i> (larval “nests” in Katsuragi)
<i>Cirsium japonicum</i>	+	–	–	ns for <i>A. hyperbius</i> , <i>C. erate</i> , <i>P. machaon</i> , <i>C. cardui</i> , <i>V. indica</i>
<i>Erigeron philadelphicus</i>	+	–	–	ns for <i>P. machaon</i> , <i>A. hyperbius</i>
Urticaceae				
<i>Boehmeria nivea</i>	+	–	–	fp for <i>C. cardui</i> and <i>V. indica</i>
Aristolochiaceae				
<i>Asarum asperum</i>	+	–	+	fp for <i>L. japonica</i>
Fabaceae				
<i>Trifolium repens</i>	++	+	+	fp for <i>C. erate</i> ; ns (Katsuragi) for <i>C. erate</i> , <i>A. hyperbius</i> , <i>L. boeticus</i> , <i>C. cardui</i> , <i>P. machaon</i> , <i>L. phlaeas</i> ; ns (Medake) for <i>L. boeticus</i>
<i>Trifolium pratense</i>	++	–	–	fp for <i>C. erate</i> ; ns (Katsuragi) for the same species as in <i>T. repens</i>
<i>Sophora flavescens</i>	+	–	–	fp for <i>L. boeticus</i>
<i>Lespedeza cyrtobotrya</i>	++	+	+	fp for <i>L. boeticus</i> ; ns for <i>L. boeticus</i> , <i>P. guttata</i> , <i>C. cardui</i> , <i>P. machaon</i>
<i>Lespedeza bicolor</i>	++	–	–	fp for <i>L. boeticus</i> ; ns for the same species as in <i>L. cyrtobotrya</i>
<i>Pueraria lobata</i>	+	–	–	fp for <i>L. boeticus</i>
Polygonaceae				
<i>Rumex acetosa</i>	+	–	–	fp for <i>L. phlaeas</i>
Ulmaceae				
<i>Zelkova serrata</i>	+	–	–	fp for <i>N. xanthomelas</i> , <i>V. indica</i>
Gramineae				
<i>Miscanthus sinensis</i>	++	–	–	fp for <i>P. guttata</i>
<i>Setaria faberi</i>	–	+	+	fp for <i>P. guttata</i>
Liliaceae				
<i>Erythronium japonicum</i>	+	–	–	ns for <i>L. japonica</i>
<i>Lilium lancifolium</i>	+	–	–	ns for <i>P. machaon</i> , <i>A. hyperbius</i>
<i>Lilium auratum</i>	+	–	–	ns for <i>P. machaon</i> , <i>A. hyperbius</i>
Rubiaceae				
<i>Galium verum</i> var. <i>asiaticum</i>	+	–	–	ns for <i>P. machaon</i> , <i>A. hyperbius</i>
Caryophyllaceae				
<i>Dianthus superbus</i> var. <i>longicalycinus</i>	+	–	–	ns for <i>P. machaon</i> , <i>A. hyperbius</i>
Ericaceae				
<i>Pieris japonica</i>	–	++	–	ns for <i>P. xuthus</i> , <i>P. machaon</i> , <i>A. hyperbius</i>
<i>Rhododendron indicum</i>	+	++	–	ns (Medake) for <i>P. xuthus</i> , <i>P. machaon</i> , <i>A. hyperbius</i> , <i>P. bianor</i>
<i>Rhododendron macrosepalum</i>	+	+	+	ns for <i>P. bianor</i> and <i>P. machaon</i> in spring on Odake (circle OS6)

Table 2. List of observed species from the slope, subsummit and summit areas of Mt Katsuragi and Mt Nijo (Mt Katsuragi=K; Mt Nijo: Medake=M, Odake=O).

species	K	M	O	species	K	M	O
Papilionidae				<i>Pelopidas mathias</i>	+	–	–
<i>Graphium sarpedon</i>	+	+	+	<i>Polytremis pellucida</i>	+	+	–
<i>Luehdorfia japonica</i>	+	–	–	<i>Potanthus flavum</i>	+	+	–
<i>Papilio bianor</i>	+	+	+	<i>Thoressa varia</i>	+	–	–
<i>Papilio helenus</i>	+	+	+	Nymphalidae			
<i>Papilio machaon</i>	+	+	+	<i>Araschnia burejana</i>	+	–	–
<i>Papilio protenor</i>	+	+	+	<i>Argynnis paphia</i>	+	+	+
<i>Papilio xuthus</i>	+	+	+	<i>Argyreus hyperbius</i>	+	+	+
<i>Seracinus montela</i>	+	–	–	<i>Cynthia cardui</i>	+	+	+
Danaidae				<i>Cyrestis thyodamas</i>	+	–	+
<i>Parantica sita</i>	+	+	+	<i>Dichorragia nesimachus</i>	+	+	+
Pieridae				<i>Fabriciana adippe</i>	+	–	–
<i>Colias erate</i>	+	+	+	<i>Hestina japonica</i>	+	+	+
<i>Eurema hecabe</i>	+	+	+	<i>Kaniska canace</i>	+	+	+
<i>Pieris melete</i>	+	+	+	<i>Limenitis camilla</i>	+	+	+
<i>Pieris rapae</i>	+	+	–	<i>Limenitis glorifica</i>	+	–	–
Lycaenidae				<i>Neptis sappho</i>	+	+	+
<i>Callophrys ferrea</i>	+	+	–	<i>Nymphalis xanthomelas</i>	+	+	+
<i>Celastrina argiolus</i>	+	+	+	<i>Polygonia c-aureum</i>	+	+	–
<i>Curetis acuta</i>	+	+	–	<i>Sasakia charonda</i>	–	+	–
<i>Everes argiades</i>	+	–	–	<i>Vanessa indica</i>	+	+	+
<i>Japonica lutea</i>	+	+	–	Libytheidae			
<i>Lampides boeticus</i>	+	+	+	<i>Libythea celtis</i>	+	+	+
<i>Lycaena phlaeas</i>	+	+	–	Satyridae			
<i>Narathura japonica</i>	+	+	–	<i>Lethe diana</i>	+	+	+
<i>Pseudozizeeria maha</i>	+	+	+	<i>Melanitis phedima</i>	+	–	–
<i>Spindasis takanonis</i>	+	–	–	<i>Minois dryas</i>	+	–	–
Hesperiidae				<i>Mycalesis francisca</i>	+	+	+
<i>Choaspes benjaminii</i>	+	–	–	<i>Mycalesis gotama</i>	+	+	–
<i>Daimio tethys</i>	+	+	+	<i>Neope goschkevitschii</i>	+	+	+
<i>Erynnis montanus</i>	+	+	+	<i>Ypthima argus</i>	–	+	+
<i>Parnara guttatta</i>	+	+	–	Total: 55 spp.	53	42	31

c) Discrimination of hilltopper / non hilltopper

The definition of (non)hilltoppers was realized according to the following assumptions. On Mt Katsuragi, when the $\Sigma\%$ VISIT (=frequency of visits) of the 30 circles belonging to the “broad summit” equals 75%, the species is randomly distributed on the hill (*cf.* $30/40 \times 100=75\%$) and is thus a non hilltopper. When the $\Sigma\%$ VISIT for the same circles is less than 75%, then the species is concentrated on the bottom of slopes and is also a non hilltopping species. Finally, a percentage higher than 75% means hilltopping for the species considered. On Mt Nijo, when $\Sigma\%$ VISIT in the broad summit circles is equal or less than 77% (*i. e.* $20/26 \times 100$), the species is a non hilltopper. When the percentage is greater than 77%, it is a hilltopper.

Results and discussion

A total of 55 species were observed, with 29 species shared by the 3 peaks (Table 2). Among them, 53 and 43 species (8 families) were on Mt Katsuragi 2001–2002 and on Mt Nijo 2002, respectively. On Mt Nijo, 42 species were recorded on Medake whereas only 31 on Odake (Table 2). The number of species found on Mt Nijo is inferior to that recorded by

Hiura (1976), namely 65 species. However, Hiura (1976) walked a transect route comprising not only the mountain itself but also a wide area of countryside at its foot.

In Table 3 and Figs 3a–c, the mean number of visits (exhaustive version including foraging data, female counts and counts beyond the mating activity schedule) and rank order for the 10 dominant species present on each hilltop in a particular season and subzone were shown. The divergences from mountain to mountain in the most dominant species in each season and subzone, despite the fact that 41 species from the total list are shared between both mountains, may reflect differences in vegetation structure (*e. g.* brightness of transect sections; Greatorex-Davies *et al.*, 1993) or composition as well as (micro)climate on each mountain.

a) real hilltoppers

1. *Papilio machaon*

In Table 4, no Chi-Square test was done with Katsuragi 2001 data for this species because no counts at all were recorded on the slope transect. In Nijo 2002, the test result was significant. Hence, in both years, *P. machaon* distributionally belonged to the hilltopper category. On the summit, it was abundant from spring to autumn and first dominant species on Mt Katsuragi (2001–2002 except spring 2001) and Odake (Figs 3a–c, Table 3). By contrast, it was the first dominant on Medake only in spring and its abundance neatly decreased there from spring to autumn (Figs 3a–c, Table 3).

2. *Papilio xuthus*

The result of the Chi-Square goodness-of-fit test (Nijo 2002 in Table 4) was significant: distributionally, this species was classified as a hilltopper. On Medake summit, it was the most abundant in spring and the least abundant in autumn. It was the second dominant species after *P. machaon* in spring and though it became the 3rd and 5th dominant in summer and autumn, respectively, its ranking position just after *P. machaon* remained the same in the 3 seasons. Despite being present on Mt Katsuragi summit, it did not belong to the 10 dominant species and, on Odake summit, though classified among the 10 dominant species in summer and autumn (rank 7), its abundance was excessively low (Figs 3a–c, Table 3).

3. *Papilio helenus*

No Chi-Square test was done (Nijo 2002 in Table 4) because no counts at all were recorded on the slope transect. This species belongs thus, distributionally, to the hilltopper category. It was not present on the summit of Mt Katsuragi and only as a trace on the subsummit area. In Medake summit, it was scarce and among the 10 dominant species only in spring (rank 8), though present in each season on the summit. In Odake summit, it was scarce though among the 10 dominant species in the 3 seasons (ranks 7 in spring, 4 in summer, 7 in autumn) (Figs 3a–c, Table 3).

4. *Papilio bianor*

No Chi-Square test was done (Nijo 2002 in Table 4) because no counts at all were recorded on the slope transect. This species was thus, distributionally, a hilltopper. In Mt Katsuragi 2001–2002, it was only present as a trace on the summit (Figs 3a–c), though among the 10 dominants in spring 2002 (Table 3). In contrast, it was relatively abundant in spring on Medake and Odake summits and was there the 4th and 3rd dominant species, respectively. It was still classified there among the 10 dominants in summer and autumn, though it had become (very) scarce in those seasons (Figs 3a–c, Table 3).

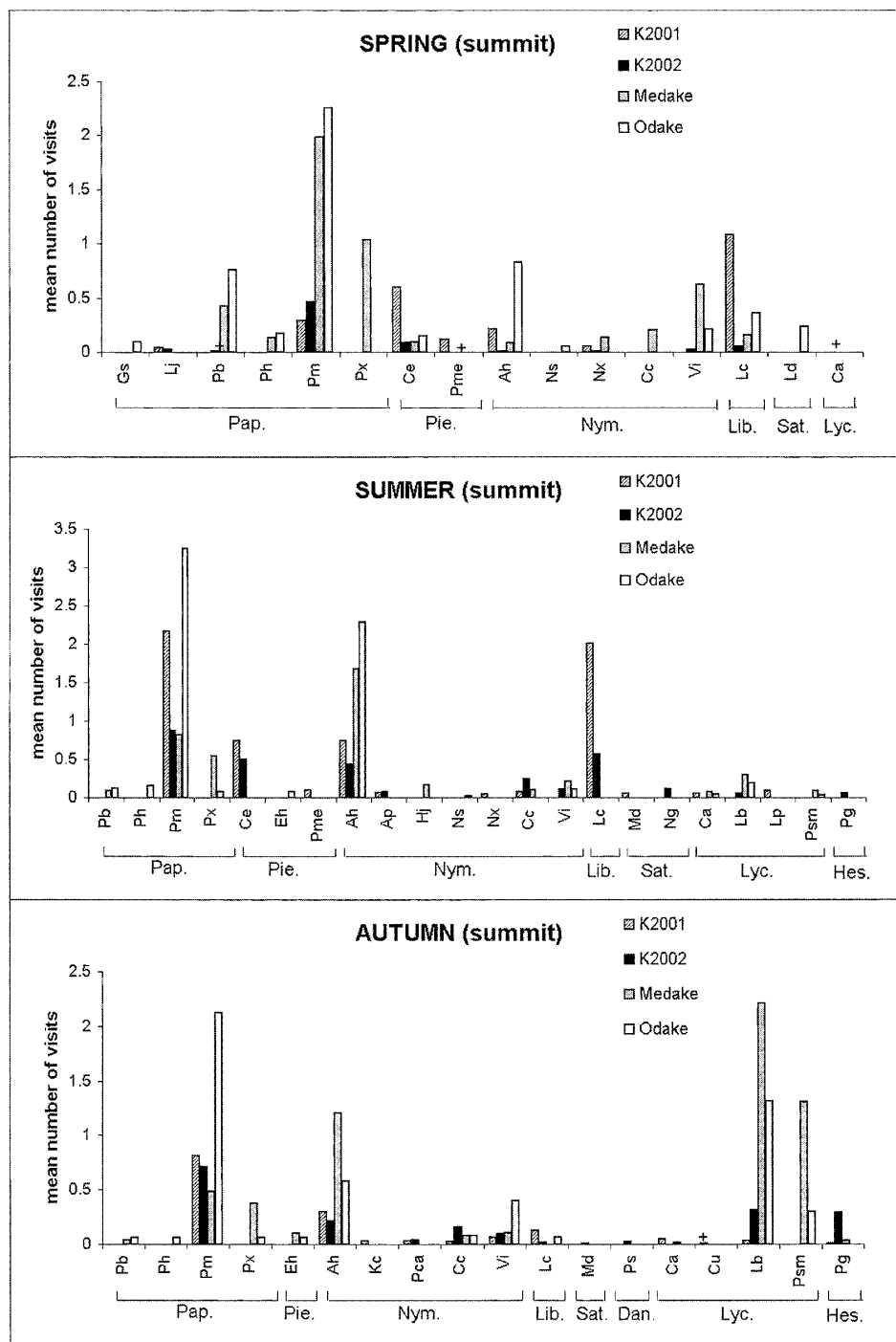


Fig. 3. Quantitative representation of the information mentioned in Table 3 (with some additional species to compensate the fact that, sometimes, several species belong to the same rank level or when one species may have been overestimated because of its easy confusion in flight with another similar-looking species). a: summit; b: subsummit; c: slope. Sub B, C, D=circles 21–23, 24–26 and 27–28, respectively. Pap=Papilionidae; Pie=Pieridae; Nym=Nymphalidae; Lib=Libytheidae; Sat=Satyridae; Dan=Danidae; Lyc=Lycenidae; Hes=Hesperiidae; +=trace abundance (indicated when not visible at the graph scale).

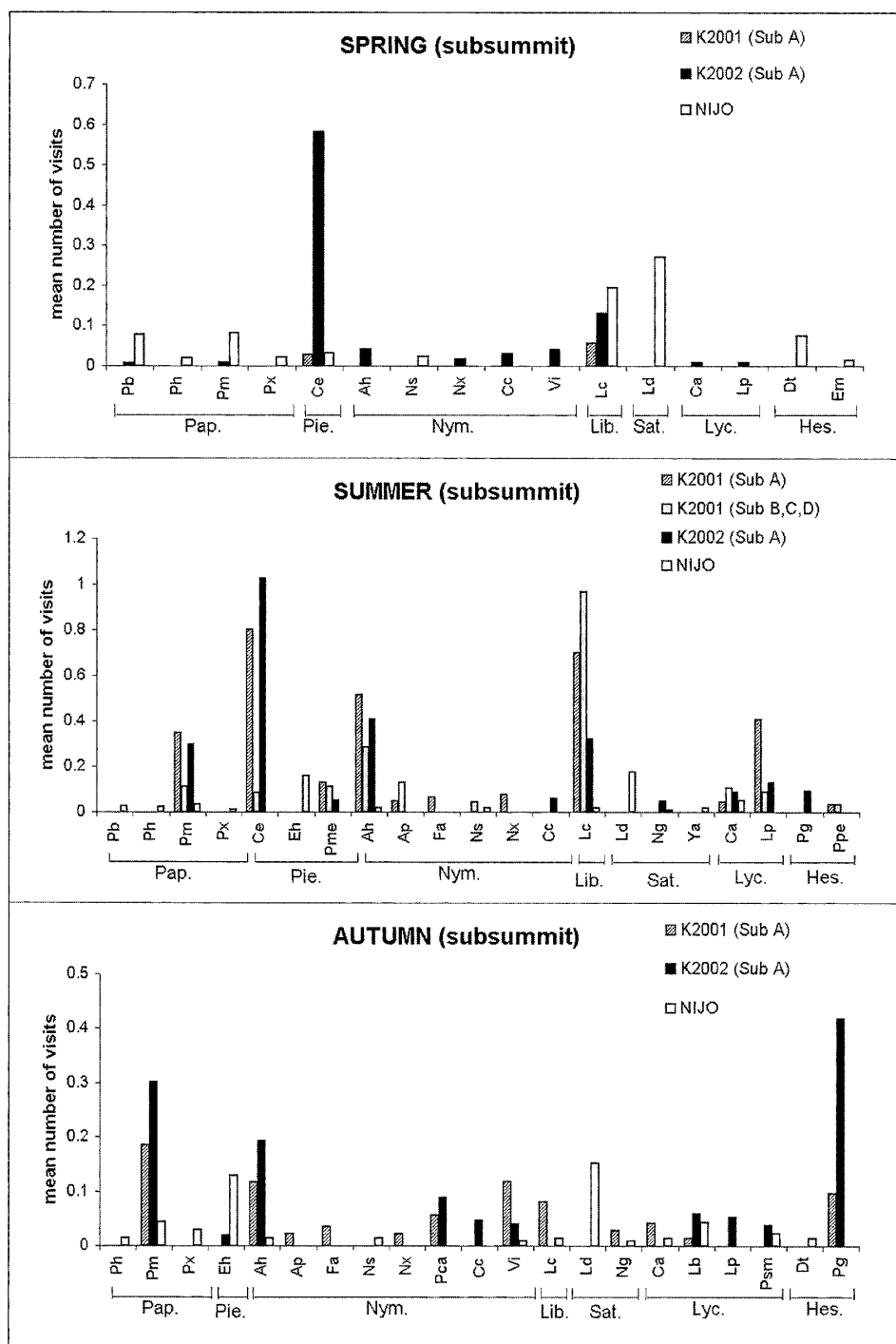


Fig. 3 (continued). See caption on p.117.

5. *Luehdorfia japonica*

In Table 4, this species could not be statistically proven to be a hilltopper because of too few data in Katsuragi 2001 and no comparative data in Nijo 2002. It was very scarce in spring on Mt Katsuragi summit, though among the 10 dominant species (rank 7 in 2001 and rank 5 in 2002) and it was totally absent on Mt Nijo's summits, subsummit and slope (Figs 3a-c, Table 3).

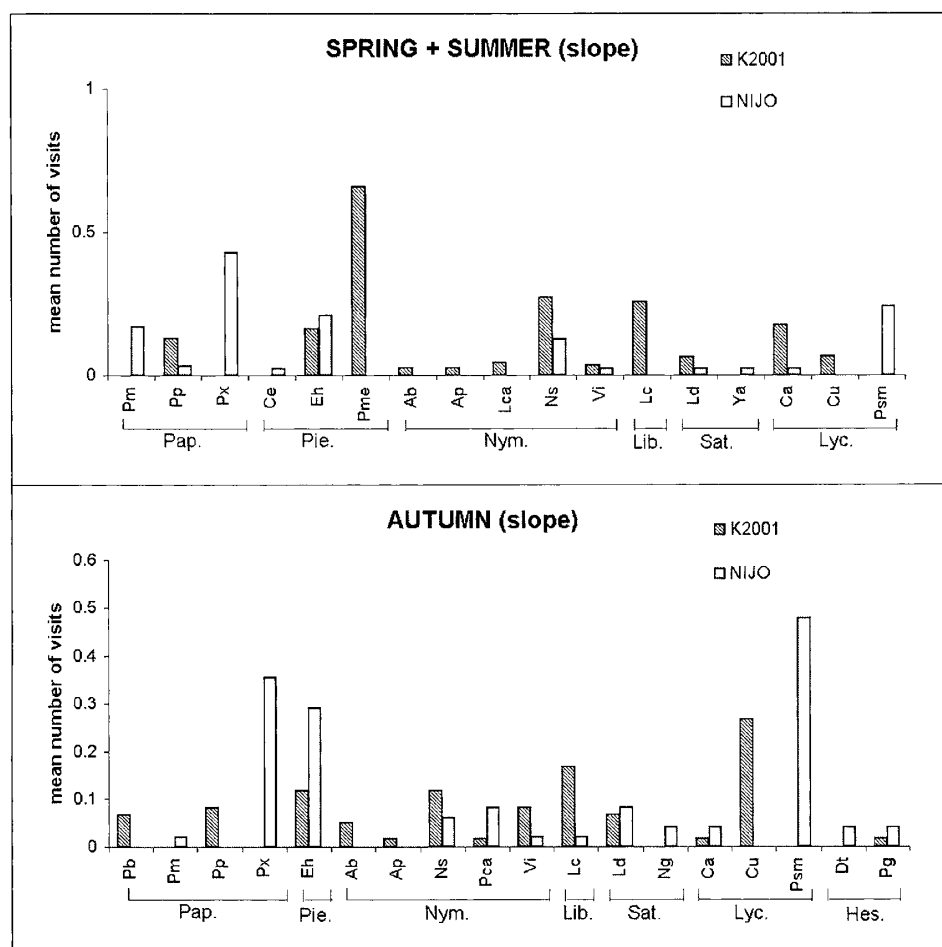


Fig. 3 (continued). See caption on p.117.

6. *Argyreus hyperbius*

In Table 4, no Chi-Square tests were done for this species because only one count was recorded on the slope transects of Katsuragi 2001 and Nijo 2002, respectively. On both mountains, this species can thus be classified, distributionally, as a hilltopper. On Mt Katsuragi summit, it was relatively and more or less equally abundant in summer and autumn of both years, rare in spring 2001 and very rare in spring 2002. On Medake summit, it was also very rare in spring but much more abundant in summer and autumn than in Mt Katsuragi and more abundant in summer than in autumn. On Odake summit in summer, the abundance was still higher than on Medake and decreased sharply in autumn, reaching the summer-autumn abundance level of Mt Katsuragi. In contrast with Medake and Mt Katsuragi, the abundance in spring on Odake summit was relatively high. It should also be noted that, in any season on Katsuragi and Odake summits, its dominance ranking order was just after or many ranks after *P. machaon*, whereas it was the reverse situation on Medake summit (except spring). For instance, *A. hyperbius* was the 1st dominant species in summer on Medake summit while *P. machaon* was the 1st dominant on Odake and Katsuragi summits at that season (Figs 3a-c, Table 3).

7. *Cynthia cardui*

In Table 4 (Nijo 2002), no Chi-Square test was done because no counts at all were recorded

Table 3. Ranking dominance status of the 10 most abundant species on each hilltop in a particular season and subzone. Species with an identical mean number of visits are cited together at the same rank level, separated by oblique bars.

Order	Spring				Summer				Autumn			
Summit	K2001	K2002	Medake	Odake	K2001	K2002	Medake	Odake	K2001	K2002	Medake	Odake
1	Lc	Pm	Pm	Pm	Pm	Pm	Ah	Pm	Pm	Pm	Lb	Pm
2	Ce	Ce	Px	Ah	Lc	Lc	Pm	Ah	Ah	Lb	Psm	Lb
3	Pm	Lc	Vi	Pb	Ce	Ce	Px	Lb	Lc	Pg	Ah	Ah
4	Ah	Vi	Pb	Lc	Ah	Ah	Lb	Ph	Vi	Ah	Pm	Vi
5	Pme	Lj	Cc	Ld	Pme	Cc	Vi	Pb	Ca	Cc	Px	Psm
6	Nx	Nx	Lc	Vi	Lp	Ng	Hj	Vi	Lb/Kc/ Pca	Vi	Eh/Vi	Cc
7	Lj	Ah	Nx	Ph	Cc	Vi	Cc	Px/Eh	–	Pca	–	Ph/Lc/ Eh/Px/ Pb
8	–	Pb	Ph	Ce	Ap	Ap	Pb	–	–	Ps	Cc	–
9	–	Pme/Ca	Ce	Gs	Ca/Md	Pg	Psm	Ca	Cc	Lc	Pb	–
10	–	–	Ah	Ns	–	Lb	Ca	Psm	Pg	Md	Pg	–
Subsum.	K2001 (Sub A)	K2002 (Sub A)	NIJO		K2001 (Sub A)	K2001 (others)	K2002 (Sub A)	NIJO	K2001 (Sub A)	K2002 (Sub A)	NIJO	
1	Lc	Ce	Ld		Ce	Lc	Ce	Ld	Pm	Pg	Ld	
2	Ce	Lc	Lc		Lc	Ah	Ah	Eh	Vi	Pm	Eh	
3	–	Ah	Pm		Ah	Ap	Lc	Ca	Ah	Ah	Pm/Lb	
4	–	Vi	Pb		Lp	Pme	Pm	Pm	Pg	Pca	–	
5	–	Cc	Dt		Pm	Pm	Lp	Pb	Lc	Lb	Px	
6	–	Nx	Ce		Pme	Ca	Pg	Ph	Pca	Lp	Psm	
7	–	Lp/Ca	Ns		Nx	Lp	Ca	Ns/Ya/ Lc/Ah	Ca	Cc	Ah/Ph/Ca/Ns/ Dt/Lc	
	–	–	Px									
8	–	Pm	Ph		Fa	Ce	Cc	–	Fa	Vi	–	
9	–	Pb	Em		Ap	Ns	Pme	–	Ng	Psm	–	
10					Ca	Ppe	Ng	–	Ap/Nx	Eh	–	
Slope	K2001*		NIJO*		K2001		NIJO		K2001		NIJO	
1	Ns		–		Pme		Px		Cu		Psm	
2	Pp		–		Ns		Psm		Lc		Px	
3	Ld		–		Lc		Eh		Eh/Ns		Eh	
4	Lc		–		Ca		Pm		–		Ld/Pca	
5	Eh/Pme/Lca		–		Eh		Ns		Pp/Vi		–	
6	–		–		Pp		Pp		–		Ns	
7	–		–		Cu		Ld/Ca/Ce/Ya/Vi		Ld/Pb		Dt/Pg/Ng/Ca	
8	–		–		Ld		–		–		–	
9	–		–		Lca		–		Ab		–	
10	–		–		Vi		–		Pca/Ca/Ap/Pg		–	

K=Mt Katsuragi; Subsum. =subsummit; Sub A=circles 12–20; others=circles 21–28 (see Figs 3a–c); * =insufficient data (from only 1 day in K2001) or no available data at all (in NIJO). Abbreviations for the species cited in this table and Figs 3a–c: Ab=*Araschnia burejana*; Ah=*Argyreus hyperbius*; Ap=*Argynnis paphia*; Ca=*Celastrina argiolus*; Cc=*Cynthia cardui*; Ce=*Colias erate*; Cu=*Curetis acuta*; Dt=*Daimio tethys*; Eh=*Eurema hecabe*; Em=*Erynnis montanus*; Fa=*Fabriciana adippe*; Gs=*Graphium sarpedon*; Hj=*Hestina japonica*; Kc=*Kaniska canace*; Lb=*Lampides boeticus*; Lca=*Limenitis camilla*; Lc=*Libythea celtis*; Ld=*Lethe diana*; Lj=*Luehdorfia japonica*; Lp=*Lycaena phlaeas*; Md=*Minois dryas*; Ng=*Neope goschkevitschii*; Ns=*Neptis sappho*; Nx=*Nymphalis xanthomelas*; Pb=*Papilio bianor*; Pca=*Polygonia c-aureum*; Pg=*Parnara guttata*; Ph=*Papilio helenus*; Pme=*Pieris melete*; Pm=*Papilio machaon*; Pp=*Papilio protenor*; Ppe=*Polytremis pellucida*; Psm=*Pseudozizeeria maha*; Ps=*Parantica sita*; Px=*Papilio xuthus*; Vi=*Vanessa indica*; Ya=*Ypthima argus*.

Table 4. Discrimination of hilltopping and non hilltopping species by Chi-square test.

Species	No. visits		Chi-Square	df	Significance	Σ% VISIT in the “Broad Summit” circle	Category of species
	SM	SL					
Katsuragi 2001							
<i>P. machaon</i>	1092	0	ND	—	—	100% > 75%	H
<i>A. hyperbius</i>	501	1	ND	—	—	99.8% > 75%	H
<i>L. celtis</i>	1121	46	778	29	0.000 (S)	96.1% > 75%	H
<i>C. erate</i>	427	0	ND	—	—	100% > 75%	H
<i>L. phlaeas</i>	147	2	1508	8	0.000 (S)	98.7% > 75%	H
<i>P. melete</i>	87	92	105	12	0.000 (S)	48.6% < 75%	NH
<i>N. sappho</i>	11	45	824	7	0.000 (S)	19.6% < 75%	NH
Nijo 2002							
<i>P. machaon</i>	1115	9	848	19	0.000 (S)	99.2% > 77%	H
<i>P. xuthus</i>	291	41	196	20	0.000 (S)	87.6% > 77%	H
<i>P. helenus</i>	64	0	ND	—	—	100% > 77%	H
<i>P. bianor</i>	169	0	ND	—	—	100% > 77%	H
<i>H. japonica</i>	35	0	ND	—	—	100% > 77%	H
<i>A. hyperbius</i>	816	1	ND	—	—	99.9% > 77%	H
<i>N. xanthomelas</i>	23	0	ND	—	—	100% > 77%	H
<i>C. cardui</i>	47	0	ND	—	—	100% > 77%	H
<i>V. indica</i>	197	0	ND	—	—	100% > 77%	H
<i>L. boeticus</i>	405	0	ND	—	—	100% > 77%	H

ND=not done (unnecessary); H=hilltopper; NH=non hilltopper; SM=broad summit; SL=slope; df=degree of freedom; S=test significant for $\alpha=0.05$ and $\alpha=0.01$.

on the slope transect. This species was thus, distributionally, a hilltopper. Data from Mt Katsuragi in 2001 and spring 2002 for that species and *V. indica* cannot be fully trusted and interpreted because the by far most preferred circle was not yet present at that time, biasing strongly the abundance and ranking orders in Figs 3a–c and Table 3. Though rarer than *A. hyperbius*, *C. cardui* is still relatively abundant in summer and autumn in Mt Katsuragi and ranked before *V. indica*. The tendency is opposite on Medake summit during the same two seasons and also in spring as well as for Odake summit in autumn, with *V. indica* preceding *C. cardui* in dominance status and *C. cardui* having become a very rare species. In spring and summer on Odake summit, *C. cardui* was not observed at all (Figs 3a–c).

8. *Vanessa indica*

In Table 4 (Nijo 2002), no Chi-Square test was done because no counts at all were recorded on the slope transect. This species belongs thus, distributionally, to the hilltopper category. This species is rarer than *C. cardui* on Mt Katsuragi (at least in summer and autumn), while the reverse is true on Medake and Odake summits in all seasons. In spring and summer on the summit, *V. indica* was more abundant on Medake than on Odake while the opposite trends occurred in autumn (Figs 3a–c).

9. *Nymphalis xanthomelas*

In Table 4 (Nijo 2002), no Chi-Square test was done because no counts at all were recorded on the slope transect. This species was thus, distributionally, a hilltopper. It was very rare though among the 10 dominant species in spring on Mt Katsuragi (2001–2002: rank 6) and Medake (rank 7). It was present in summer on Mt Katsuragi 2001 and 2002, though not among the 10 dominants, but absent from Medake and Odake summits at that season as well as in autumn on the 3 peaks (Figs 3a–c).

10. *Lampides boeticus*

In Table 4 (Nijo 2002), no Chi-Square test was done because no counts at all were recorded on the slope transect. This species was thus, distributionally, a hilltopper. On the 3 peaks, this late season species was consistently absent in spring and among the most abundant and dominant species in autumn (except in Katsuragi 2001). Its low abundance in 2001 on Mt Katsuragi summit is possibly because its highly targeted distribution on certain shrubs was overlooked at that time. In autumn, it was the 1st dominant on Medake, preceding *A. hyperbius* and *P. machaon*, whereas it was the 2nd dominant species on Katsuragi 2002 and Odake, ranking between *P. machaon* and *A. hyperbius*. The autumnal recorded abundance in Mt Katsuragi was much lower than on Odake and Medake (highest) summits. In summer season on the 3 peaks, it was rare (especially in Mt Katsuragi) and its dominance status was (well) behind *P. machaon* and *A. hyperbius* (rank 10 in Katsuragi 2002, rank 4 in Medake and rank 3 in Odake) (Figs 3a–c and Table 3).

11. *Parnara guttata*

In Table 4, it could not be statistically proven to be a hilltopper because of too few data in Katsuragi 2001 and no comparative data in Nijo 2002. However, *P. guttata* was quite abundant in autumn 2002 (268 counts, including foraging individuals, or 66 counts, excluding them) on the summit of Mt Katsuragi and might, at first glance, be thought of as a potential candidate for hilltopping. This late season species was, as *L. boeticus*, absent in spring on the 3 peaks and most abundant in autumn, at least in Katsuragi 2002. However, in Katsuragi 2001, it was abnormally scarce in autumn, possibly simply because of its being overlooked by the still inexperienced observer. Only a trace presence was noticed on Medake summit in autumn (rank 10 in dominance) and it was absent in autumn on Odake summit as well as in summer on Medake and Odake summits. On Mt Katsuragi 2002 in summer, it was very scarce and its dominance status (rank 9) was nearly equivalent (similar abundances) to *L. boeticus*, though just before it. It should be noted that in autumn in Katsuragi 2002, the dominance rank was also nearly equivalent to *L. boeticus*, though just after it (Figs 3a–c, Table 3).

b) controversial hilltoppers

In the distributional results (Table 4), *Hestina japonica*, *Libythea celtis*, *Colias erate* and *Lycaena phlaeas* were considered as hilltoppers whereas only *L. phlaeas* is known as an occasional hilltopper in the Japanese literature (Kawazoé and Wakabayashi, 1976). Shields (1967) also pointed out that the genera *Colias* and *Lycaena* are seemingly devoid of hilltopping species in North America, as well as the subfamily Libytheinae. We need thus some more behavioural evidence to definitively discount those species as hilltoppers such as mark (summit)-release (downslope)-recapture (summit) experiments.

1. *Hestina japonica*

In Table 4 (Nijo 2002), no Chi-Square test was done because no counts at all were recorded on the slope transect. This species can thus, distributionally, be classified as a hilltopper. It was not recorded at all in Katsuragi 2001–2002 on the summit and only a trace presence existed on Odake summit. On Medake summit, it was absent in spring, rare in summer with a dominance rank just behind *V. indica*, and only a trace in autumn (Figs 3a–c, Table 3).

2. *Libythea celtis*

In Table 4 (Katsuragi 2001), the result of the Chi-Square goodness-of-fit test was significant. This species belonged, distributionally, to the hilltopper category. It was exces-

sively abundant on Mt Katsuragi summit in spring and summer 2001. In those seasons, it was the 1st and 2nd dominant species, respectively (before *P. machaon* or just after it). In Katsuragi 2002, its abundance had considerably decreased on the summit (10 times lower in spring and 4 times in summer) but it still remained among the 3 most dominant species on that hilltop (3rd and 2nd positions, respectively) (Figs 3a–c, Table 3). In autumn 2001–2002, this species was (very) rare on Katsuragi's hilltop, though much rarer (trace) and having a much lower dominance status in 2002 (rank 9 in 2002 vs rank 3 in 2001). In spring, its abundance on the summit in Medake 2002 was roughly similar to that in Katsuragi 2002 but its dominance rank was much lower in Medake (rank 6) than in Katsuragi (rank 3). On Odake summit in spring, it was relatively rare though more abundant than in Katsuragi 2002 and its dominance rank was nearly similar on both peaks (3rd in Katsuragi, 4th in Odake). The biggest difference between the two mountains occurred in summer: absence on Medake and Odake summits but relatively abundant on Katsuragi summit in 2002, with a rank 2 of dominance. In autumn, it was absent on Medake summit and present only as a trace on Odake, though still somewhat more abundant than in Katsuragi 2002 at that season (Figs 3a–c).

3. *Colias erate*

In Table 4 (Katsuragi 2001), no Chi-Square test was done because no counts at all were recorded on the slope transect. This species can thus, distributionally, be classified as a hilltopper. It was absent in autumn on the 3 peaks. On Mt Katsuragi summit, it was relatively abundant and as abundant in spring as in summer 2001. Its abundance in Katsuragi 2002 on the summit remained the same in summer but decreased 5 times in spring 2002 (Figs 3a–c). Otherwise, the dominance status in both seasons remained the same between the 2 years (rank 2 in spring, rank 3 in summer) (Table 3). By contrast with spring 2001 on Katsuragi (but not spring 2002), the species was very rare on Medake and Odake summits at that season and its dominance rank was much lower than on Katsuragi (rank 9 and 8 on Medake and Odake, respectively, vs rank 2 on Katsuragi). The biggest difference between the 2 mountains occurred in summer with no counts at all recorded on Mt Nijo while the species was relatively abundant on Mt Katsuragi summit (Figs 3a–c).

4. *Lycaena phlaeas*

The result of the Chi-Square goodness-of-fit test (Katsuragi 2001) was significant (Table 4): distributionally, this species was classified in the hilltopper category. In Katsuragi 2001, it was relatively abundant and the 4th dominant species on the subsummit in summer (Figs 3a–c, Table 3). In Katsuragi 2002, its abundance on the subsummit in summer had sharply decreased (roughly 4 times) but it was still the 5th dominant species there. On the summit of Mt Katsuragi, it was very rare in summer 2001 and only the 6th dominant species there. In summer 2002, it was not even among the 10 dominant species on Katsuragi summit and its presence was a trace. On Medake summit, it was also present only as a trace in summer and absent from Odake summit. *L. phlaeas* was mostly observed in summer on both mountains, except some trace data on the subsummit of Mt Katsuragi in other seasons (Figs 3a–c).

c) non hilltoppers

The results of the Chi-Square goodness-of-fit test (Katsuragi 2001) for both species were significant (Table 4): they distributionally belonged to the non hilltopper category. In Kawazoé and Wakabayashi (1976), *Pieris melete* and *Neptis sappho* are also considered as non hilltoppers.

Acknowledgements

We wish to express our sincere thanks to Mr N. Hirai and Dr T. Hirowatari of Osaka Prefecture University for their helpful advice and assistance. This work was supported by a Japanese Government (Monbukagaku-sho) scholarship and in part by Grant-in-Aids from the Japan Ministry of Education, Culture, Sports, Science and Technology (no. 15510193).

References

- Alcock, J., 1983. Territoriality by hilltopping males of the great purple hairstreak, *Atlides halesus* (Lepidoptera, Lycaenidae): convergent evolution with a pompilid wasp. *Behav. Ecol. Sociobiol.* **13**: 57–62.
- , 1984. Convergent evolution in perching and patrolling site preferences of some hilltopping insects of the Sonoran Desert. *Swest. Nat.* **29** (4): 475–480.
- , 1985. Hilltopping in the nymphalid butterfly *Chlosyne californica* (Lepidoptera). *Am. Midl. Nat.* **113** (1): 69–75.
- , 1987. Leks and hilltopping in insects. *J. nat. Hist.* **21**: 319–328.
- Alcock, J. and D. Gwynne, 1988. The mating system of *Vanessa kershawi*: males defend landmark territories as mate encounter sites. *J. Res. Lepid.* **26**: 116–124.
- Alcock, J. and K. M. O'Neill, 1986. Density-dependent mating tactics in the Grey hairstreak, *Strymon melinus* (Lepidoptera:Lycaenidae). *J. Zool., Lond. (A)* **209**: 105–113.
- Bitzer, R. J. and K. C. Shaw, 1979(80). Territorial behavior of the Red Admiral, *Vanessa atalanta* (L.) (Lepidoptera: Nymphalidae). *J. Res. Lepid.* **18**: 36–49.
- Brown, W. D. and J. Alcock, 1990(91). Hilltopping by the Red Admiral Butterfly: mate searching alongside congeners. *J. Res. Lepid.* **29**: 1–10.
- Dennis, R. L. H. and W. R. Williams, 1987. Mate location behavior of the Large Skipper butterfly *Ochlodes venata*: flexible strategies and spatial components. *J. Lepid. Soc.* **41**: 45–64.
- Greatorex-Davies, J. N., Sparks, T. H., Hall, M. L. and R. H. Marrs, 1992. The influence of shade on butterflies in rides of coniferised lowland woods in southern England and implications for conservation management. *Biol. Conserv.* **63**: 31–41.
- Hiura, I., 1976. A consideration on the butterfly fauna and its transformation in the lowland of Osaka and Nara, central Japan. *Shizenshi-Kenkyu* **1** (10): 189–206 (in Japanese).
- Kawazoé, A. and M. Wakabayashi, 1976. *Coloured Illustrations of the Butterflies of Japan*. Hoikusha Publishing.
- Kemp, D. J., 2001. Investigating the consistency of mate-locating behavior in the territorial butterfly *Hypolimnas bolina* (Lepidoptera:Nymphalidae). *J. Insect Behav.* **14**: 129–147.
- Lederhouse, R. C., 1982. Territorial defense and lek behavior of the Black Swallowtail butterfly, *Papilio polyxenes*. *Behav. Ecol. Sociobiol.* **10**: 109–118.
- New, T. R., 1993. Introduction to the biology and conservation of the Lycaenidae. In New, T. R. (Ed.), *Conservation Biology of Lycaenidae (Butterflies)*: 1–21. (Occasional Paper of the IUCN Species Survival Commission 8). IUCN, Gland, Switzerland.
- Pinheiro, C. E. G., 1990(91). Territorial hilltopping behavior of three swallowtail butterflies (Lepidoptera, Papilionidae) in Western Brazil. *J. Res. Lepid.* **29**: 134–142.
- Rutowski, R. L. and J. Alcock, 1989. Insect mating systems in the Sonoran Desert of North America. *J. arid Envir.* **17**: 157–165.
- Scott, J. A., 1968(70). Hilltopping as a mating mechanism to aid the survival of low density species. *J. Res. Lepid.* **7**: 191–204.
- , 1974. Mate-locating behavior of butterflies. *Am. Midl. Nat.* **91**: 103–117.
- , 1975. Mate-locating behavior of Western North American butterflies. *J. Res. Lepid.* **14**: 1–40.
- Shields, O., 1967. Hilltopping. *J. Res. Lepid.* **6**: 69–178.
- Siegel, S. and N. J. Jr. Castellan, 1988. *Nonparametric Statistics for the behavioural Sciences* (2nd Edn). McGraw-Hill International Editions.
- Turner, J. D., 1990. Vertical stratification of hilltopping behavior in swallowtail butterflies (Papilionidae). *J. Lepid. Soc.* **44**: 174–179.
- Wickman, P.-O., 1988. Dynamics of mate-searching behaviour in a hilltopping butterfly, *Lasiommata megera* (L.): the effects of weather and male density. *Zool. J. Linn. Soc.* **93**: 357–377.
- Williams, M., 1994. *Butterflies of Southern Africa: a Field Guide*. Southern Book Publishers.

摘 要

大阪・奈良府県境の2つの山稜における山頂占有性チョウ類の識別と季節消長 (Sophie NAVEZ・石井 実)

山頂占有性チョウ類を識別するとともに、その季節消長を明らかにするために、大阪と奈良の府県境に位置する葛城山 (= 大和葛城山, 標高 960 m) および二上山 (2つのピーク, 雄岳 517 m と雌岳 474 m) の山頂, 亜山頂, 斜面に、それぞれ 46, 26 個の半径 5 m の架空の円形調査地を設定した。葛城山では 2001 年および 2002 年, 二上山では 2002 年に春から秋まで調査を行い、定量化のために 5 分間の調査時間内に各観察円を訪れた平均回数を用いた。葛城山から 53 種, 雌岳で 42 種, 雄岳で 31 種, 合計 55 種 (8 科) が確認され、そのうち 29 種が 3 つのピークで共通に見られた。2 つの山のいずれにおいても、これらの種の大部分は低頻度であった。2001 年の葛城山の調査においては、統計的に「広義の山頂」(山頂および亜山頂) に分布が偏っていたキアゲハ, ツマグロヒョウモン, テングチョウ, モンキチョウ, ベニシジミを山頂占有性種と分類した。しかし、後者の 3 種については、検討の余地が残されている。2002 年の二上山の調査では、アカタテハ, ヒメアカタテハ, キアゲハ, ナミアゲハ, カラスアゲハ, モンキアゲハ, ヒオドシチョウ, ツマグロヒョウモン, ウラナミシジミ, ゴマダラチョウが山頂占有性であった。これらすべての種は葛城山でも記録されたが、2001 年と 2002 年の結果からナミアゲハ, カラスアゲハ, モンキアゲハ, ゴマダラチョウは、葛城山では山頂占有性とはみなされなかった。それ以外の上記のすべての二上山における山頂占有性種は、葛城山でも山頂占有性であった (2001 年または 2002 年の結果)。逆に、イチモンジセセリとギフチョウは、2002 年の調査結果から葛城山においてのみ山頂占有性とみなされたが、二上山ではギフチョウは記録そのものがなかった。二上山では、モンキチョウ, ベニシジミ, テングチョウは山頂占有性種ではなかった。また、ナミアゲハ, ゴマダラチョウ, ヒメアカタテハは雌岳では山頂占有性を示したが、雄岳では違っていた。一部の山頂占有性種は、3 シーズン (キアゲハ), 2 シーズン (ツマグロヒョウモンは夏と秋, モンキチョウとテングチョウは春と夏) あるいは 1 シーズンのみ (ウラナミシジミとイチモンジセセは秋), 山頂において数多く見られたが、3 つのピーク間で優占順位は異なっていた。一方、アカタテハなど数種の山頂占有性種は、ピーク間で相対的な密度や優占順位は異なるものの、3 シーズンを通じてどのピークでも少なかった。

(Accepted July 9, 2006)